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Development of the third eye in the lizard Sceloporus occidentalis

by

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With seven text figures.

Dedicated to Professor Fritz Baltzer in honor of his scientific achievements and in appreciation of his personal kindness to the author.

Although the morphogenesis of the reptilian parietal (third) eye, especially its early developmental relationship to the epiphysis or pineal gland, has been studied by several investigators (see Steyn, 1957), some points remain obscure. Hopefully this paper will cast light on three of them, namely: the lateral origin of the third eye, the source of the parietal nerve, and the possible role of organizers.

MATERIALS AND METHODS

Adults and embryos of the Western Fence Lizard, *Sceloporus occidentalis*, were used in these studies, the former captured in the Berkeley hills by a noose of copper wire (Eakin, 1957), the latter developed from eggs laid in terraria by gravid females collected in the field. Serial paraffin sections stained with hematoxylin and eosin were prepared from embryos fixed in Bouin's solution at several stages of development from the formation of the primary epiphyseal diverticulum to full differentiation of the parietal eye.

The heads of two adults with anomalies of the third eye were similarly handled for light microscopy. In experiments on nerve degeneration the meninges and parietal nerve of adult lizards were cut transversely a few tenths of a millimeter posterior to the third eye by means of a microscalpel (Burch 1942), after reflection of the overlying skin. Segments of the nerve anterior and posterior to the incision were later removed, fixed in Dalton's solution (Dalton 1955) and prepared for electron microscopy following the procedures described in previous studies (Eakin and Westfall 1960; Eakin, Quay and Westfall 1961), except that the epoxy resin, Epon, and lead stains were employed.

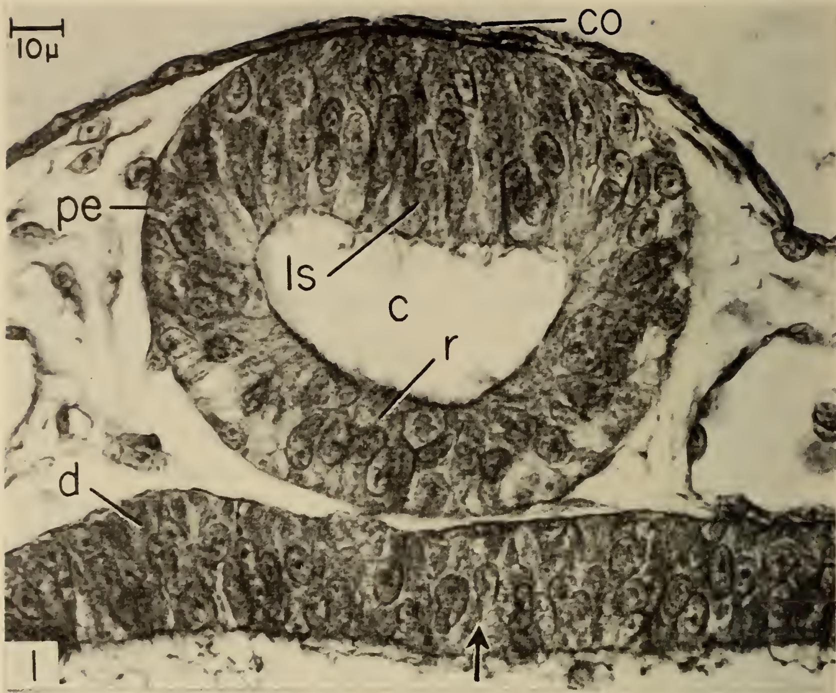
RESULTS

1. *Lateral origin of the parietal eye.* One of the embryos of *Sceloporus occidentalis* studied had been fixed at the time of constriction of the primary epiphyseal vesicle into the prospective parietal eye and the presumptive pineal organ. The stage corresponded approximately to that in *Cordylus polyzonus* described and figured by Steyn (1957) as stage C (see Steyn's Fig. 4, p. 247). Figs. 1 to 3 of this paper are cross sections of the epiphyseal diverticulum of the above embryo at the following levels: Fig. 1, through the parietal vesicle, already showing evidence of differentiation of lens (*ls*) and retina (*r*); Fig. 2, through the presumptive epiphysis just anterior to the canal connecting the pineal lumen (*c*) and the third ventricle of the diencephalon; and Fig. 3, through the zone of constriction between the parietal and pineal parts of the diverticulum. The reader will observe that the diverticulum is asymmetrical in the region of the constriction (Fig. 3), a feature which I believe to be significant. The lumen is to the left of the midline. The asymmetry of the embryo's heart and gut were used to identify right and left sides of the body. It will be observed, moreover, that much of the right wall of the tube, specifically between the two arrows, is darker than the rest of the diverticulum. That this darker part (outlined in ink) is the anterior end of the epiphysis is clear as one traces it section by section. The remainder of the tube, mostly to the left, is prospective parietal eye. Finally, the parietal vesicle itself lies slightly to the left of the midline (indi-

cated by arrow in Fig. 1), not only in this specimen but in older embryos. The parietal vesicle in *Sceloporus occidentalis*, therefore, appears to be "budded" from the left side of the epiphyseal diverticulum.

2. *Origin of parietal nerve.* It is well known that if a nerve fiber is severed the proximal segment (i. e. the part between the incision and the nerve cell body) survives and regenerates, whereas the distal segment undergoes Wallerian degeneration. Cutting the parietal nerve in a lizard and examining the pieces of the nerve anterior and posterior to the incision for degenerative changes should permit one to determine the location of the nerve cell bodies of the neurones which form the nerve. If degeneration occurs rostral to the transection, the nuclei lie in the brain. If, on the other hand, it is found caudal to the incision, the nuclei are situated in the retina of the eye. The latter alternative was shown to be true by a study of severed parietal nerves in a series of ten animals.

Fig. 4 is a low power electron micrograph of the anterior piece of a severed parietal nerve in an adult *Sceloporus occidentalis* four days postoperative. The nerve fibers are essentially normal in appearance (*cf*, Fig. 20, Eakin and Westfall 1960), except for one feature, namely, dense granules (*g*) scattered in the axoplasm of many fibers, especially the larger ones. Normally these granules are associated with stacks or whorls of cisternae (Eakin 1963), like those (*s*) seen in one fiber in Fig. 4. The posterior segment of the parietal nerve in the same animal shows marked degeneration (Fig. 5). Most of the nerve fibers have disappeared and those that remain exhibit the same pathological changes observed in Wallerian degeneration in mammals (see Glimstedt and Wohlfart 1960; Lee 1963). They are: swelling and aggregation of mitochondria (*m*), dilation of tubules or vesicles (*v*) and, in final stages of breakdown, fragmentation of organelles (*f*). The sheath cells also show changes: enlargement and probable increase in number, accumulation of small dense granules (*g*), appearance of large lipid (?) droplets (*dp*), and a marked increase in the number of pigment granules (*pg*). The last feature was observed earlier in a study of the nerve in parietalectomized lizards (Eakin and Stebbins 1959). The conclusion seems clear: the nerve cell bodies of the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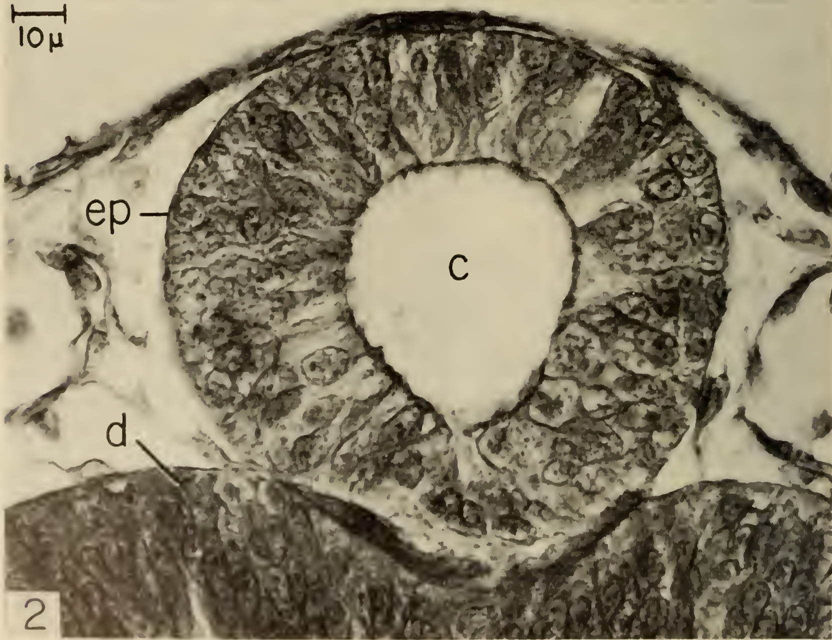
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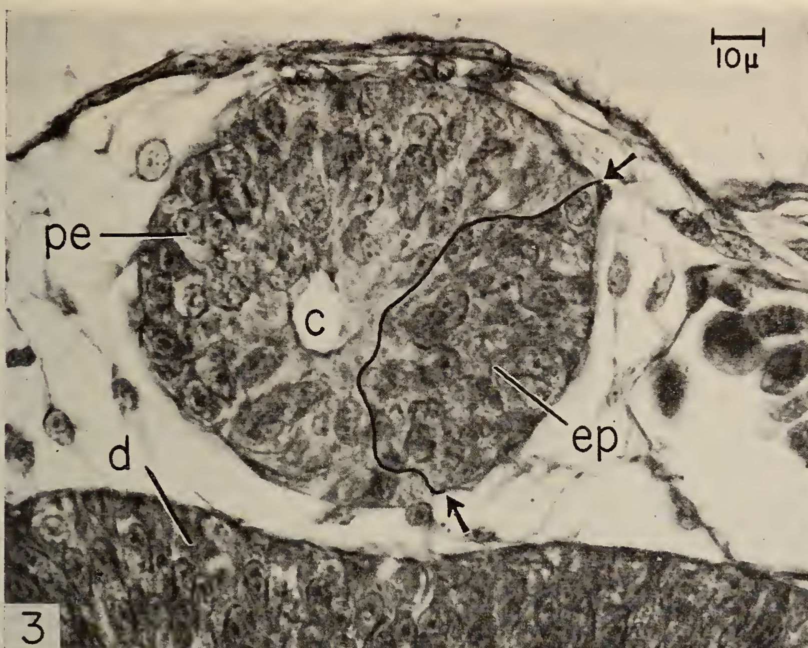

FIG. 1 and 2.

Cross-sectional views of presumptive parietal eye (Fig. 1) and pineal organ (Fig. 2) of the primary epiphyseal diverticulum in an early embryo of *Sceloporus occidentalis.*

c, lumen of the organs; *co*, prospective cornea; *d*, roof of diencephalon; *ep*, presumptive epiphysis or pineal organ; *ls*, lens of eye in early stage of differentiation; *pe*, presumptive parietal eye; *r*, future retina. Arrow on Fig. 1 indicates the midline of the embryo.

FIG. 3.

Cross-sectional view of the primary epiphyseal diverticulum of the same embryo shown in Figs. 1 and 2 at the level of junction of presumptive parietal and pineal organs.

c, cavity of diverticulum (note small size and position on the left); *d*, diencephalic roof; *ep*, anterior end of prospective epiphysis; *pe*, prospective parietal eye. Arrows and line indicate boundaries between pineal (right) and parietal (left) organs.

neurones which constitute the parietal nerve lie in the retina of the eye.

3. *A developmental anomaly.* The parietal eyes of several hundred *Sceloporus occidentalis* have been examined in one way or

another at Berkeley in recent years. Two instances of incomplete separation of the parietal and pineal divisions of the epiphyseal diverticulum have been observed. One specimen, a sub-adult male

Fig. 4.

Low power electron micrograph of anterior segment of parietal nerve of adult *S. occidentalis* four days after transection. Cross-sectional view of about half of the nerve fibers.

g, granules; *k*, bundle of collagenous fibers; *m*, mitochondria; *n*, nucleus of sheath cell; *p*, perineurium; *s*, stack of cisternae with granules.

(snout-vent length of 44 mm.), was captured by my colleague, Robert C. Stebbins, near Berkeley in the course of our study on the effects of ablation of the parietal eye (Stebbins and Eakin 1958).

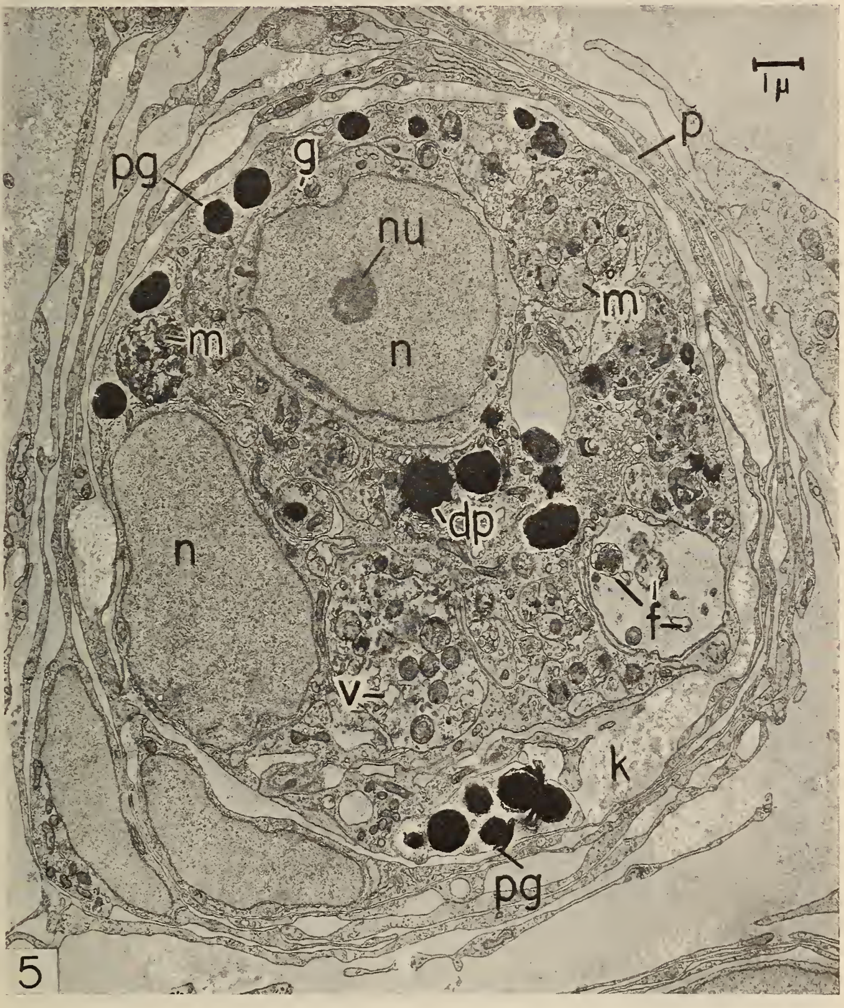

Fig. 5.

Low power electron micrograph of posterior segment of same parietal nerve shown in Fig. 4. Cross-sectional view of entire nerve.

dp, osmophilic droplet (lipid ?); *f*, fragments of organelles; *g*, small granules; *k*, collagenous fibers; *m*, mitochondria, swollen and aggregated; *n*, nuclei of sheath cells; *nu*, nucleolus; *p*, perineurium; *pg*, pigment granules; *v*, vesicles.

Stebbins' field notes contain this entry: "no parietal eye whatsoever; no corneal elevation or transparency. Lizard otherwise normal." The head of this animal was later sectioned by Dr. Robert Ortman who was then associated with us on the project. We discovered that actually a third eye was present but attached to the apex of the epiphysis (Fig. 6). Instead of separating from the pineal organ and " migrating " anteriorly to its definitive position above the cerebrum and just beneath the skin, it remained at its site of origin at the diencephalic level and inside the meninges and bony cranium. Normally, the skin above the parietal eye is differentiated into a transparent cornea, having a relatively thick epidermis and a relatively thin and loose dermis containing no chromatophores and a markedly reduced number of collagen fibers. In this specimen, however, the integument at the usual site of the parietal eye was unspecialized, consisting of normally thin epidermis and thick dermis with a full complement of collagen fibers, melanophores and lipophores (see Eakin, Quay and Westfall 1961). These features account for the lack of transparency of the parietal area noted by Stebbins in the living animal. On the other hand, a large parietal fontanelle in the roof of the cranium was present as is typical of sub-adult fence lizards.

Fig. 7 shows the ectopic parietal eye at higher magnification. It is fully differentiated into lens (*ls*), capsule (*ca*) and a retina (*r*) containing normal sensory, supportive (pigmented) and ganglion (*gc*) cells arranged in typical anatomical relationships, except at the point of attachment of the eye to the tip of the epiphysis. The zone of junction between the retina and the epiphyseal epithelium is somewhat disorganized. The parietal and pineal lumens are not continuous, but the capsules of the two organs are smoothly fused. Although the nerve fibers were not identified in the hematoxylin and eosin stained sections, I have no doubt that some of the fibers at x in Fig. 7 are axons of ganglion cells in the eye and that they extend along the anterior face of the epiphysis, the normal course of the parietal nerve.

A second specimen (not figured) was an adult male the head of which was sectioned and stained with the periodic-acid-Schiff (PAS) technique in connection with another study (Eakin, Stebbins and Wilhoft 1959). The parietal eye appeared normal under external observations, but it was found later upon micro-

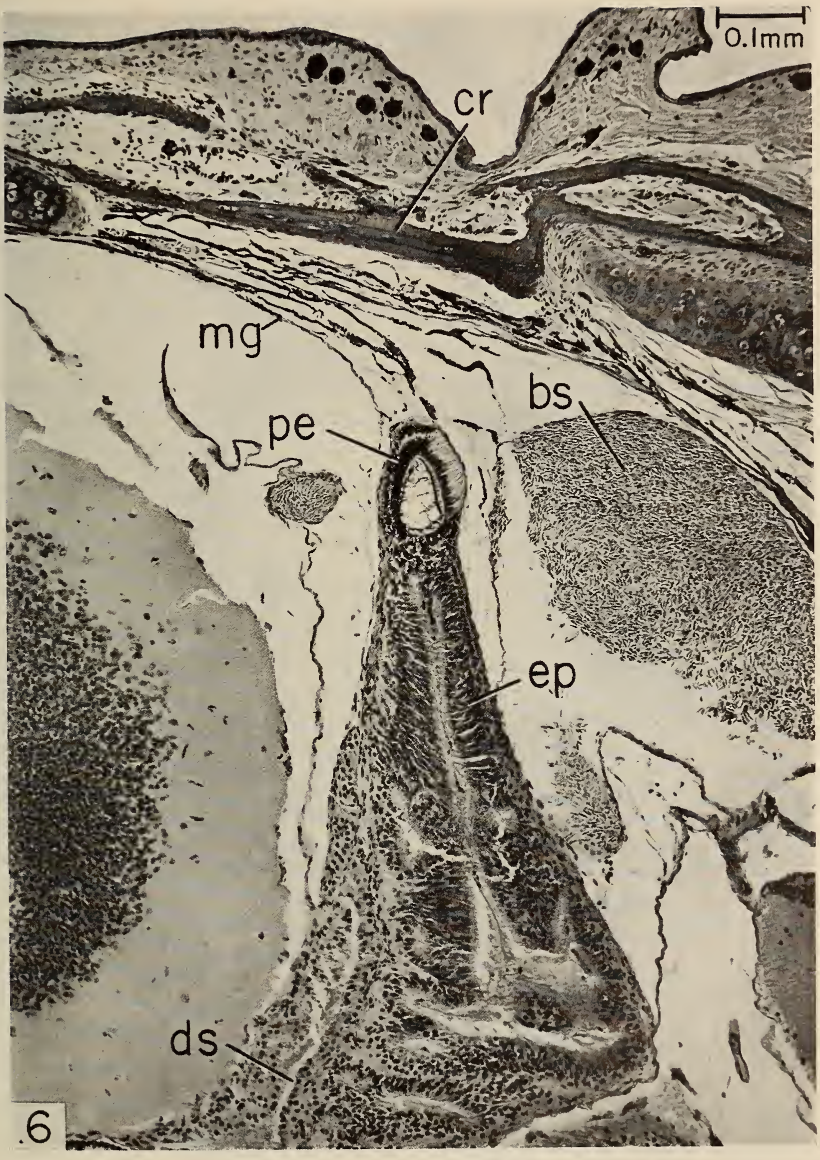

Fig. 6.

Sagittal view of epiphyseal complex of an adult *S. occidentalis* showing an ectopic parietal eye (*pe*) attached to the tip of the epiphysis (*ep*).

bs, blood sinus; *cr*, cranium; *ds*, dorsal sac; *mg*, meninges. Anterior is to the reader's left, posterior to the right.

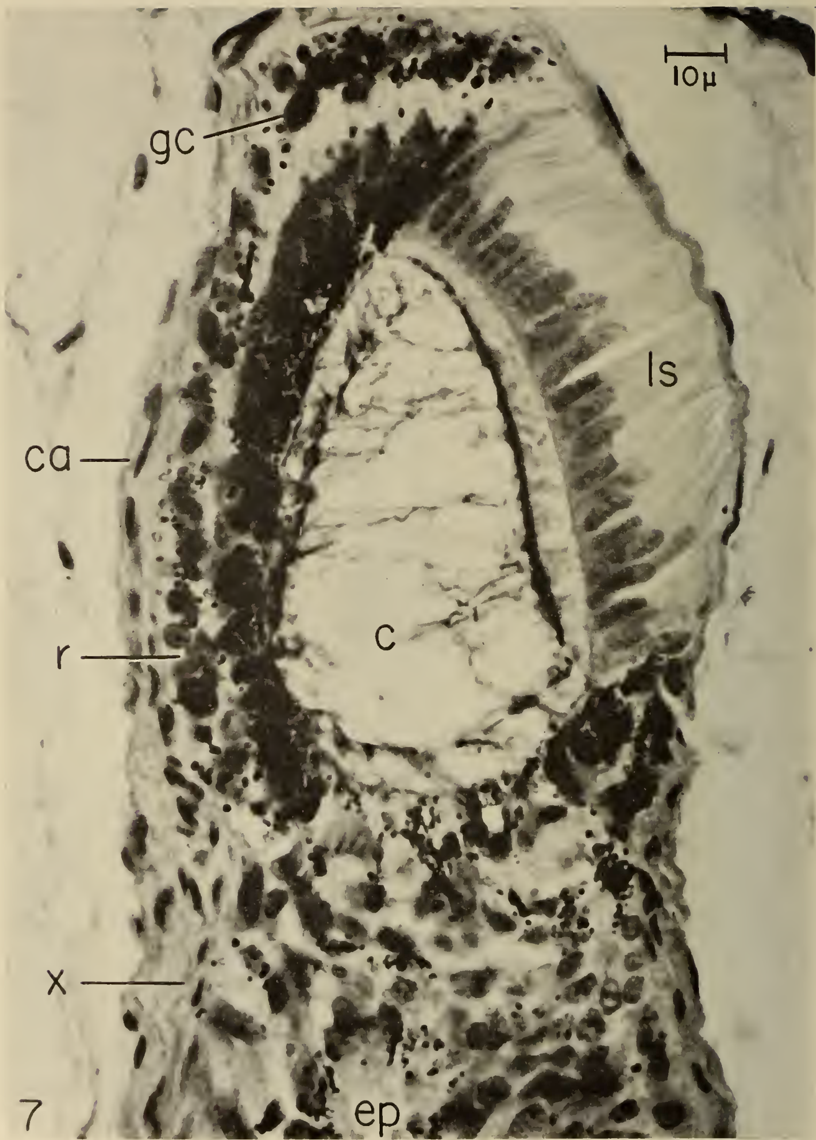

Fig. 7.
Higher magnification of the parietal eye shown in Fig. 6.
c, lumen of eye; *ca*, capsule; *ep*, tip of epiphysis; *gc*, ganglion cell; *ls*, lens; *r*, retina; *x*, fibers, some of which are probably nerve fibers (parietal nerve).

scopical examination to be connected to the tip of the epiphysis which in the course of development had become exceedingly elongated. Normally the eye lies between one to three millimeters anterior to the epiphysis. The two organs are connected by the slender parietal nerve running on the under surface of the meninges. In this specimen the epiphysis itself continued forward as a narrow tube (0.1 mm. in diameter) to within 10μ of the parietal eye. The short gap between the two organs contained connective tissue and the parietal nerve. The latter emerged from the postero-ventral surface of the eye and extended along the ventral (anterior) side of the epiphysis. Professor Stebbins has shown me some of his sections of an alligator lizard, *Gerrhonotus multicarinatus*, in which the normal relationship of epiphysis and parietal eye is very similar to that just described. The same picture is also normally found in certain other lizards (see Schmidt 1909).

DISCUSSION

Problem of symmetry. The parietal eye and its homologue in other vertebrates, such as the amphibian frontal organ, are often referred to as the parapineal organ (see Tilney and Warren 1919). The basic anatomical and developmental relationships between this body and the pineal organ have long been a subject of speculation by anatomists, embryologists, and paleontologists. Attention has been given particularly to the question: were they originally—in the ancestral vertebrate—a pair of bilaterally arranged diencephalic diverticula? Those who answer affirmatively point to the following evidence. 1. The course of the parietal nerve is to one side of the midline, whereas the pineal tract lies on the opposite side. Some investigators traced the parietal nerve along the left side of the head and into the left habenular ganglion (see Bargmann 1943); others, working usually on different species, found it on the right side and connected to the right habenular ganglion (see Gladstone and Wakeley 1940). 2. Another argument for the bilateral origin of the epiphyseal organs is the presence in the fossils of certain Devonian fishes of two foramina transversely oriented in the diencephalic region of the cranium (Edinger 1956). 3. Several workers have demonstrated that the

parietal eye and epiphysis in certain reptiles arise from separate, side-by-side evaginations of the neural tube. DENDY's work on *Sphenodon* (1911) is especially convincing. In this form the parietal eye develops on the left side as does also the parietal nerve. Bilateral epiphyseal outgrowths have been demonstrated also in fishes (HILL 1891, 1894; LOCY 1894), in amphibians (CAMERON 1903*a*), and in birds (CAMERON 1903*b*). Finally, VAN DE KAMER (1949) has shown that the median epiphyseal diverticulum in anurans is formed by the fusion of paired anlagen.

Several investigations, on the other hand, do not support the theory of bilateral origin of pineal and parapineal organs because they show that the two structures arise from a pair of diencephalic diverticula, both of which lie in the midline (see GLADSTONE and WAKELEY 1940). The anterior evagination in many reptiles becomes the parietal eye, the posterior one the epiphysis. Incidentally, STEYN (1957) correctly points out that the anterior vesicle contributes additionally to the cephalic part of the epiphysis. Other workers also cast doubt on the above theory because they trace the pineal and parapineal organs to a single median outpocketing of the forebrain (see GLADSTONE and WAKELEY 1940). I agree with STEYN (1957, p. 236) that " whether there are one or two primordia [I believe that it is largely a matter of interpretation] it appears that the development always includes a phase in which the parietal organ becomes separated from the epiphysis by a process of constriction." But this question should be raised: does the parietal vesicle exhibit any tendency toward a constriction to one side of the midline?

Most published figures showing the early stages in the development of the parapineal and pineal diverticula in reptiles present a sagittal view, which would not reveal a bilateral pairing of the two organs. DENDY (1899, 1911), as mentioned earlier, found that in *Sphenodon* " the position of the primary parietal vesicle to the left of the middle line is very remarkable, and appears to be constant " (1899, p. 114). NOWIKOFF (1910) illustrates a cross-sectional view of the epiphyseal rudiment (plate III, Fig. 2) which appears asymmetrical to me but he makes no comment on the point. In this paper I have shown that in an embryo of *Sceloporus occidentalis* the parietal vesicle was constricted from the left side of the epiphyseal diverticulum. Unfortunately only one embryo of this

critical stage was available, but in older embryos I found the parietal eye, now separate from the epiphysis, to the left of the midline. DENDY noted the same feature in *Sphenodon*. These observations plus the evidence of two side-by-side epiphyseal outgrowths in other vertebrates and the many records of the course of the parietal nerve on one side of the midline suggest to me that the parapineal and pineal organs are fundamentally bilaterally paired structures, but that in the course of evolution the rostral displacement of the former has almost obliterated its ancestral parasagittal position.

Origin of parietal nerve. The parietal nerve was described by several nineteenth century workers (e.g. STRAHL and MARTIN 1888). Contemporary investigators (e. g. STEYN 1957; ROTH and BRAUN 1958) concluded, however, that the nerve although present in the embryo degenerates in the adult. It was shown recently by light microscopy that the nerve in the adults of several lizards persists (EAKIN and STEBBINS 1959) and it was proved to be a true nerve in one of them by electron microscopy (EAKIN and WESTFALL 1960). In *Sceloporus occidentalis*, the same form used in this study, we found that the adult nerve consists of about 250 non-medullated fibers. Occasionally we find a few medullated fibers. Although the fibers were thought to be the axons of the ganglion cells this point could not be established with certainty. The developmental source of the parietal nerve still remained an unsolved problem.

Many workers (e. g. NOWIKOFF 1910) believed that the fibers of the nerve arise from ganglion cells in the retina of the third eye just as in the lateral eyes the axons of the ganglion cells form the optic nerve. Other investigators, both early (e. g. BÉRANECK 1887, 1892) and recent (e. g. STEYN 1959), thought that the parietal nerve originates in the brain. I hope that the second part of this study, namely, the electron microscopy of the severed parietal nerve in *S. occidentalis*, clearly establishes the retina of the third eye as the source of the fibers in the nerve. The segment of the nerve posterior to the point of severance degenerated following surgery, whereas the anterior segment (i. e. between the incision and the eye) was essentially normal. Were the nerve cell bodies of these neurones situated in the brain, one would expect the reverse picture: degeneration anterior to the cut, normal nerve posteriorly.

The precise origin of the nerve fibers is probably the ganglion cells, which can be identified by the large size of their nuclei (*gc*, Fig. 7) and by certain cytological and cytochemical characteristics (Eakin, Quay and Westfall 1961). In *S. occidentalis* it is estimated that there are about 250 of these cells in the retina of the parietal eye, each sending an axon into the parietal nerve (Eakin 1960). Although the possibility that some fibers come directly from photoreceptoral cells (see Fig. 10 in Trost 1953) has not been excluded, it seems unlikely to me.

Developmental anomalies. The two instances of abnormal development of the parietal eye described here permit one to draw the following conclusions regarding the developmental mechanics of the organ. 1. The differentiation of the eye is not dependent upon the attainment of its normal definitive position above the telencephalon, external to the meninges, and in intimate association with the integument (see Fig. 2 of Stebbins and Eakin 1958, or Fig. 1 of Eakin and Westfall 1959). One observes that all cell types in the ectopic eye shown here (Figs. 6 and 7) develop fully and in typical morphological relationships with one another even though the organ failed to separate from the epiphysis and lies below the meninges and bony cranium at the diencephalic level of the brain. Schmidt (1909) described an embryo of *Lacerta vivipara* in which a parietal vesicle although still attached to the epiphysis was differentiating a lens. Schmidt's description is very brief and his figure is only an outline drawing. I conjecture, however, that had that *Lacerta* embryo completed development the picture of its epiphyseal complex would have been very similar to the one presented here.

2. The second conclusion is a corollary of the first: the parietal eye appears to be a self-differentiating system. By that I do not exclude the possibility of inductive factors operative before or at the time of formation of the primary epiphyseal diverticulum. It seems to me, however, that the third eye arises from an independent and definitely circumscribed anlage. Not only does the ectopic eye figured here exhibit normal differentiation morphologically, histologically, and cytologically, but the boundary between eye and epiphysis is clear except for the connective tissue capsules of the two organs which blend smoothly, and with the exception of some irregularities in the retina at the zone of junction with the

epiphysis. The latter represents, in my opinion, the effect of atypical mechanical factors, namely, those resulting from a lack of a complete capsule, rather than an integration of parietal and epiphyseal organs. In other words, I see no evidence of regulation. If the embryonic parapineal and pineal rudiments constituted a harmonious equipotential system I should expect a less distinct boundary between the two structures and an abnormally large (or small) lens or retina; but, as we see, all parts show normal proportions.

The only evidence, known to me, of possible inductive action is an instance of an abnormal epiphyseal diverticulum in *Anguis fragilis* described by Trost (1953) in which the pineal part of the primary evagination was atypically high and in contact with the presumptive epidermis. The dorsal wall of the prospective epiphysis looked like the presumptive lens of the parietal eye in normal embryos of the same age, according to Trost, because of the paucity of cells which appear to be forerunners of sensory elements. Therefore she concluded that the epidermis exercises a lens-inducing influence upon that part of the primary outpocketing which comes in contact with it. Normally this is the prospective lens of the parietal eye, but in Trost's atypical embryo it was the dorsal wall of the presumptive pineal organ. Without an examination of the actual preparations an independent judgement cannot be made, but I am not convinced from Trost's drawings that the dorsal wall of the very young epiphyseal diverticulum in her embryo is indeed differentiating into a lens. Moreover, I note in the literature figures showing both pineal and parapineal parts of the normal primary diverticulum in intimate contact with the skin ectoderm (e. g. Fig. 29 of Plate 25 in Dendy 1911 and Fig. 2 in Steyn 1957), yet a lens forms only in the parietal eye.

3. The differentiation of the cornea, on the other hand, appears to be dependent upon the inductive action of the parietal vesicle or perhaps more specifically the lens of the third eye. As we have seen in the lizard with the ectopic eye described and figured here, the integument above the normal site of the eye shows no morphological or histological features of a cornea. The reader will recall that in the development of the lateral eye the lens is an organizer for the cornea (see Mangold 1931).

SUMMARY

1. The early development of the parietal eye in the Western Fence Lizard, *Sceloporus occidentalis*, was studied by light microscopy of paraffin sections of embryos of varying age. Evidence is presented that the eye arises from the *left* side of the epiphyseal diverticulum. The ancestral relationship of the pineal and parapineal organs is discussed in the light of this observation and those of other investigators.

2. Information on the origin of the nerve fibers in the parietal nerve was obtained by electron microscopy of the severed nerve in adults of *S. occidentalis*. The segment of the nerve posterior to the transection degenerates suggesting that the nerve cell bodies of the neurones which form the nerve lie in the retina of the third eye. Thus the nerve grows from the eye to the brain.

3. Ectopic parietal eyes in two adult fence lizards were described and one of them figured. From these specimens certain inferences regarding the developmental mechanics of the eye were made: *a)* The anlage of the eye is definite, circumscribed, and self-differentiating. *b)* The eye is not a harmonious-equipotential system. *c)* The cornea is induced by the parietal vesicle.

ZUSAMMENFASSUNG

Bei der Zauneidechse *(Sceloporus occidentalis)* entsteht das Parietalauge aus einer Ausstülpung der embryonalen Gehirnwand, welche auf der linken Seite der primären Epiphysenanlage abgeschnürt wird. Da nach Durchtrennung des Parietalnerven elektronenmikroskopisch keine Degenerationserscheinungen im proximalen Abschnitt des Nerven gefunden wurden, muss man annehmen, dass die Fasern des Parietalnervs ihren Ursprung im dritten Auge haben und von dort in das Gehirn auswachsen. Es werden ferner zwei Fälle von abnormer Entwicklung des Parietalauges beschrieben; bei diesen fehlt die Cornea. Verf. nimmt an, dass die Determination des Parietalauges früh erfolgt, dass aber der auslösende Faktor für die Corneabildung wahrscheinlich in der Linse zu lokalisieren ist.

RÉSUMÉ

L'oeil pinéal du Scélopore occidental *(Sceloporus occidentalis)* se développe à partir d'une évagination de la paroi embryonnaire du cerveau. Cette évagination se sépare, du côté gauche de l'ébauche épiphysaire. La section des nerfs pinéaux n'entraîne aucune dégénérescence, décelable au microscope électronique, dans la partie proximale du nerf. Il faut donc en conclure que les fibres du nerf pinéal proviennent du troisième œil et se dirigent de là vers le cerveau.

L'auteur décrit deux cas d'yeux pinéaux anormaux, n'ayant point de cornée. Il admet que la détermination de l'œil pariétal est précoce et que l'agent inducteur de la cornée se trouve probablement dans le cristallin.

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